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Letter to the Editor

The Novel Components of the Arabidopsis Light Signaling Pathway May Define a Group of General Developmental Regulators Shared by Both Animal and Plant Kingdoms

Arabidopsis seedling development can follow two contrasting morphogenetic patterns depending on ambient light environments, skotomorphogenesis in darkness and photomorphogenesis in light (Deng, 1994). Mutations in 10 essential and pleiotropic Arabidopsis loci result in dark-grown seedlings that mimic light-grown wild-type seedlings (Wei et al., 1994a; Miséra et al., 1994). The recessive nature of these mutations implies that the corresponding wild-type gene products act to repress photomorphogenesis in darkness. The genes for four of these loci, *COP1* (Deng et al., 1992), *COP9* (Wei et al., 1994b), *COP11* (also named *FUS6*; Castle and Meinke, 1994), and *DET1* (Pepper et al., 1994), have been cloned. At the time they were reported, their gene products revealed either a novel combination of known protein motifs, as for COP1, or completely novel proteins, as for COP9, COP11, and DET1. As the switch between skotomorphogenic and photomorphogenic growth is uniquely a plant phenomenon, it was plausible to suggest that the light-controlled developmental switch is also unique to plants. The discovery of these novel proteins further supported the involvement of plant-specific regulatory mechanisms. However, recent advances have revealed animal proteins highly homologous to COP1, COP9, COP11, and DET1. We argue here that these proteins may represent members of larger protein families found in diverse organisms and that understanding their cellular and biochemical functions may reveal a novel development switch mechanism fundamental to both plant and animal kingdoms.

The most striking homology was found between COP11 and COP9 and their human counterparts (Figure 1). Arabidopsis COP11 is a 50 kDa hydrophilic protein that is either a component of the nuclear localized COP9 complex or is necessary for its formation or stability (Castle and Meinke, 1994; Wei et al., 1994b; our unpublished data). Recently, a human gene highly similar to *COP11*, *GPS1* (GenBank accession number U20285), has been cloned as a suppressor of a yeast *gpa1* mutant (K. S. Bowdish and J. Colicelli, personal communication). Yeast *gpa1* mutants are defective in the α subunit of the trimeric G protein that is involved in the yeast pheromone response pathway and result in cell cycle arrest at the late G1 phase during mating (Dietzel and Kurjan, 1987; Miyajima et al., 1987). The predicted amino acid sequence of GPS1 shares 47% identity and 64% similarity over the entire length with COP11 when three gaps (18, 14, and 9 residues) are introduced in the sequence alignment (Figure 1A). Although the exact function of human GPS1 is unknown, overexpression of the carboxyl half of the protein suppressed the phenotype of yeast *gpa1* mutants. This observation may imply that human GPS1 has a role in trimeric G protein signaling and cell cycle control. Although COP11 has not yet been shown to suppress the yeast *gpa1* mutation, the high degree of amino acid sequence identity would suggest that COP11 and GPS1 are homologous proteins.

In addition to human *GPS1*, two other genes have been identified whose predicted amino acid sequences share

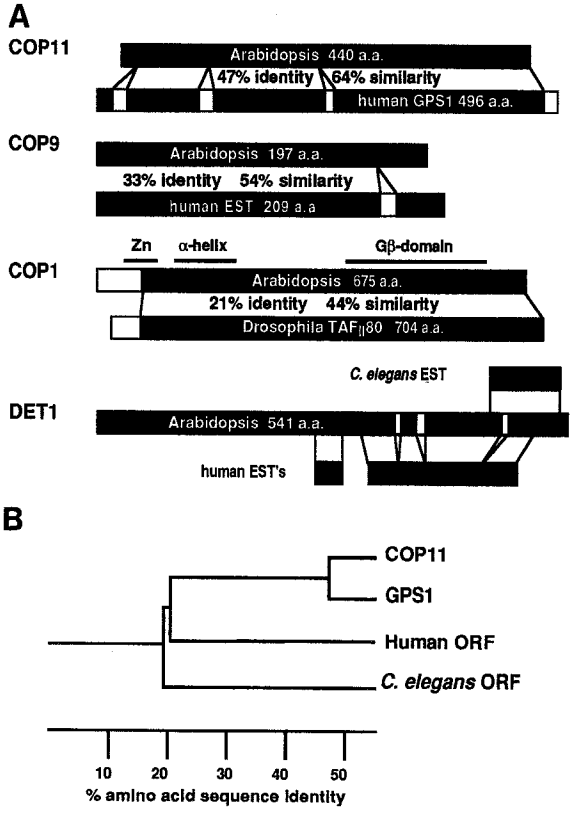

Figure 1. Summary of Amino Acid Comparisons between Arabidopsis *COP* and *DET* Gene Products and Their Animal Relatives or Homologs

(A) Comparison of Arabidopsis COP1, COP9, COP11, and DET1 and their close human or animal counterparts. For each alignment, the percentage of amino acid sequence identity and similarity and the position of gaps (shown as open boxes) are indicated. The predicted amino acid sequence for the human COP9 homolog was determined after assembling a complete coding sequence from 21 different sequences found in the dbEST database (Boguski et al., 1993; our unpublished data). The *DET1*-related EST sequences of human (GenBank accession numbers R35600, T89036, and F01468) and C. elegans (GenBank accession number D35362) were retrieved from the dbEST database and share 19%–20% identity and >40% similarity with DET1.

(B) Relationship of the COP11-like proteins. Both Arabidopsis COP11 and its human homolog GPS1 share ~20% identity and 42% similarity with the entire predicted protein sequences of a C. elegans ORF (GenBank accession number P34481) and a human ORF (GenBank accession number D14663). The C. elegans and human ORFs also share a similar degree of identity and similarity to each other.

considerable sequence similarity with COP11 (Figure 1B). Two unidentified open reading frames (ORFs), one from Caenorhabditis elegans (Wilson et al., 1994) and the other from human (GenBank accession number D14663), show ~20% identity over their entire lengths with both COP11 and GPS1 and also 20% identity among themselves. Therefore, COP11 and GPS1 probably define a family of related proteins.

COP9 is a component of a large, multisubunit nuclear protein complex whose conformation or size is subjected to light modulation (Wei et al., 1994b; our unpublished data). Twenty overlapping human expressed sequence tag (EST) sequences revealed an ORF whose predicted protein sequence has 33% identity and 54% similarity to COP9 with one 17 residue gap in the sequence alignment (Figure 1A). Since the sequence identity distribution is uniform over the entire length of the protein and the two predicted proteins are of similar size, it is possible that they may represent homologous proteins between Arabidopsis and human.

COP1 contains three known structure motifs, a Zn-binding RING finger domain in the amino terminus, a central coiled-coil region, and the WD40 repeats of the Gβ domain of trimeric G proteins in its carboxyl half. While these domains in and of themselves are not unique, COP1 remains the only protein identified thus far that contains all three. The cloning of the Drosophila TFIID subunit $TAF_{II}80$ revealed that it shares significant amino acid sequence similarity to COP1 (Dynlacht et al., 1993; see Figure 1A). This sequence similarity extends for the entire length of $TAF_{II}80$ and includes most of the length of COP1, excluding the RING finger Zn-binding motif. While these two proteins do share considerable sequence similarity, they are unlikely functional homologs since $TAF_{II}80$ does not have the distinct RING finger-type Zn-binding domain. Further, it is expected that $TAF_{II}80$ is a nuclear protein, while the nuclear localization of COP1 is subjected to light regulation (von Arnim and Deng, 1994). However, the observed sequence similarity may suggest that COP1 can interact with the general transcriptional machinery and thus regulate gene expression to repress photomorphogenesis in the dark.

DET1 is a 62 kDa hydrophilic nuclear protein (Pepper et al., 1994). Three human and one C. elegans EST clones contain predicted amino acid sequences that are similar to regions of DET1 (Figure 1A). The four EST sequences do not cover the entire coding sequence of DET1, but the similarities (19%–20% identity and >40% similarity) detected do suggest that other DET1-related proteins can be found in the animal kingdom.

The central question, though, is this: in which developmental processes do these proteins participate in nonplant organisms? The available information suggests that the *COP* and *DET* gene products play an important role in developmental regulation in plants. Perhaps these proteins are involved in fundamental cellular function, such as general transcriptional regulation, and plants have adapted this for mediating light control of a developmental switch. Plant information can now be applied to the cognate animal genes to find out whether these Arabidopsis genes represent an ancient general regulatory pathway. If so, it will be clear that plants like Arabidopsis are as suitable as models of human cellular processes as are yeast and flies.

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